

Influence of food supply and shore height on the survival and growth of the barnacle *Balanus glandula* (Darwin)

Sarah E. Gilman*, Rhiannon L. Rognstad¹

The W. M. Keck Science Department of Claremont McKenna, Scripps, and, Pitzer Colleges, 925 N. Mills Ave, Claremont, CA 91711, USA

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ABSTRACT

The contribution of energy limitation to patterns of intertidal zonation and vertical range limits is not well understood. Higher vertical positions on an intertidal shore are typically associated with greater temperature and desiccation stress during emersion; yet, organisms at higher shore heights also experience reduced feeding time and thus also face greater energy limitation than their lower shore counterparts. Disentangling the roles of abiotic stress and food limitation is critical to accurately predicting intertidal species' responses to climate change. This experiment manipulated food supply and shore height for the intertidal barnacle *Balanus glandula* (Darwin 1854). Adults were maintained in the field for 39 days at one of four shore heights spanning the species' upper vertical range limit, with or without supplemental feeding during high tides. Higher shore animals showed significantly lower growth and higher mortality relative to those lower on the shore. Across all shore heights, fed animals had significantly higher overall growth (20–27% greater final body mass), but not survival, than animals in the control treatments. No significant interactions between height and feeding treatment were detected, although the benefits of supplemental feeding tended to be smaller at higher shore heights. Our results suggest that food limitation occurs across a large portion of *B. glandula*'s vertical range and that it can influence the success of barnacles at and above the current upper vertical limit. As such, energy limitation may play an important role in the vertical limits of many high intertidal species, and in distributional limits more broadly.

1. Introduction

The intertidal zone is defined by a steep environmental gradient in space. Over a few vertical meters, as conditions shift from fully marine to fully terrestrial, organisms experience greater durations of emersion with increasing shore height and concomitant increases in thermal extremes, desiccation stress, UV exposure, and other abiotic challenges (Foster, 1971b; Gosselin and Jones, 2010; Harley and Helmuth, 2003; Menge and Branch, 2001; Somero, 2002). Body temperatures during emersion can increase by as much 30 °C over immersion temperatures (Edney, 1953; Helmuth et al., 2006b) and desiccation may lead to 40–60% loss of body mass (Haring et al., 2002; Jones and Boulding, 1999). The abiotic stresses of emersion, particularly thermal stress, greatly influence ecological patterns in the intertidal (Connell, 1961; Somero, 2002). For example, many species' overall thermal tolerances are correlated with their vertical position on the shore (Somero, 2002; Stillman and Somero, 2000). Conspecifics living at higher shore heights often show declines in growth and fecundity (Gillmor, 1982; Petes et al., 2008) and increases in physiological stress responses (Helmuth

and Hofmann, 2001; Somero, 2012) relative to lower shore individuals. High levels of emersion stress can cause mortality in newly settled larvae and juveniles of many intertidal species (Denley and Underwood, 1979; Gosselin and Qian, 1996; Jenewein and Gosselin, 2013). Finally, the upper vertical limits of many high shore intertidal species are often attributed to tolerance of emersion stress, particularly thermal stress (Connell, 1961; Foster, 1971a; Levinton, 2014; but see Underwood, 1980). The large number of documented effects of temperature, in particular, on organismal performance and species interactions has led many to suggest temperate intertidal systems as models for studying species' responses to climate change (Gilman, 2017; Helmuth et al., 2006a; Somero, 2012).

A key unanswered question lies in understanding the mechanism by which temperature limits individual success and vertical distribution on intertidal shores. Specifically, are organisms limited directly by the thermal sensitivities of their physiological systems or indirectly by the energetic costs of maintaining those systems under exposure to thermal stress (Somero, 2002)? The physiological mechanisms underlying responses to thermal stress in intertidal animals have been described in

* Corresponding author.

E-mail address: sgilman@kecksci.claremont.edu (S.E. Gilman).

¹ Present address: University of California at Santa Barbara Marine Science Institute, Building 520, Santa Barbara, CA 93106, USA.

great detail at the whole-organism, organ, cellular, protein, and genomic levels (e.g., Hofmann and Todgham, 2010; Sokolova and Portner, 2001; Somero, 2012; Stillman and Somero, 2000). Yet, several lines of evidence suggest that intertidal animals may be limited more by energetics than by their physiological limits of temperature. First, thermal tolerances measured under laboratory conditions, where animals presumably have unlimited access to food, often exceed recorded field temperatures (e.g., Denny and Harley, 2006; Wolcott, 1973), suggesting that animals have the physiological capacity to survive abiotic stresses well above those typically experienced within their vertical distribution. Indeed, both vertical and geographic distributional limits appear to occur below absolute thermal limits (Menge and Branch, 2001; Pörtner and Farrell, 2008; Sokolova et al., 2012; Tagliarolo and McQuaid, 2015), which is consistent with energetic limitations on tolerance (Pörtner, 2010; Sokolova et al., 2012). Second, the survival of newly settled larvae can be influenced both by the magnitude of emersion stress experienced and larval energy state (Emlet and Sadro, 2006), indicating a role for energetics in modulating the thermal tolerance of new recruits and juveniles. Third, a reduced food supply has been linked to lower growth in laboratory studies of animals under emersion stress (e.g., Fitzgerald-Dehoog et al., 2012; Schneider et al., 2010) and to reduced physiological defenses in the field (Dahlhoff and Menge, 1996; Dowd and Somero, 2013). Finally, high shore individuals show signs of energy limitation even in the absence of significant thermal stress (Gillmor, 1982). This occurs because, as emersion durations increase with shore height, opportunities for feeding are reduced. While some species compensate with higher feeding rates in high shore individuals (Ritz and Crisp, 1980), most cannot (Bayne et al., 1988; Underwood, 1984). Consequently, high shore animals likely experience the double challenge of increased demand for energy to sustain physiological responses to thermal stress and decreased opportunities for energy intake.

Together these points provide strong evidence that energetics influence both the success of high shore organisms and their upper vertical limits. However, to our knowledge, no study has yet demonstrated that augmenting an individual's available energy can improve its success on the high shore. Here we report the results of a field manipulation designed to specifically test whether increased food availability can improve the success of high shore adults of the intertidal barnacle *Balanus glandula*. This species is a common mid to high shore barnacle in the northeastern Pacific, acting as a foundation species on rocky shores (Glynn, 1965). Its exact vertical distribution varies by site, but is known to extend above the mean higher high tide line in both California and Washington (Connell, 1970; Glynn, 1965), meaning that upper shore individuals may be exposed to air for > 24 h during some portions of a tide series. Reduced performance at high shore heights has been linked to emersion stress in several barnacle species (e.g., Barnes and Powell, 1953; Berger et al., 2006), but feeding limitation has also been invoked (Barnes and Powell, 1953). We used a transplant experiment to examine whether an increased food supply allows for greater growth or survival of individuals and whether the relative benefit of increased food varies with shore height. We hypothesized that individuals living closer to the species' upper vertical limit would show the greatest improvements in growth and survival from supplemental feeding, as those individuals have the most restricted feeding times.

2. Methods

2.1. Study sites

Balanus glandula were collected from the mouth of Alamitos Bay, Los Angeles County, California (33.749°N, 118.113°W), southeast of the Alamitos Bay Marina. In southern California *B. glandula* occur from above the mean higher high tide to below mussel beds (Reish, 1995, S. Gilman, pers. obs.). Barnacles (mean opercular length 4.1 mm ± 0.95

SD) were collected from the middle portion of this distribution, by collecting mussels (*Mytilus galloprovincialis* and *M. californianus*) with epizooic *B. glandula*. The barnacle is a common epizooic of *Mytilus* spp., particularly near the mussels' upper vertical limit.

The experiment was conducted on a fixed pier at Berth 60 in the Port of Los Angeles, just inside the outer breakwater of the Port (33.720°N, 118.273°W) and approximately 15 km from the collection site. The pier faces nearly due west (250°) and thus gets full sun exposure in the afternoons. The site is not currently used for shipping. The NOAA CO-OPS program maintains a water level station (#9410660) at the site. The experiment was conducted in the spring of 2015, as that time of year combines frequent daytime low tides with warm terrestrial temperatures (Helmuth et al., 2002).

2.2. Collection, initial measurements, and deployment of barnacles

Mussels with epizooic barnacles were collected on February 5 and 6, 2015 and transported on ice to the W. M. Keck Science Department (Claremont, CA, USA). The mussels were shucked and barnacles, still attached to fragments of the mussel shell, were kept fully submerged in tanks at 18 °C for one week. To obtain a balance of barnacle sizes in each treatment, we roughly sorted the barnacles into size classes of small (mean opercular length = 3.3 mm ± 0.6 SD), medium (4.3 ± 0.6), and large (5.3 ± 0.7). Groups of five barnacles (1 large, two medium, two small) were attached in a single row to the back (unglazed side) of white 10.16 cm × 10.16 cm ceramic tiles with marine epoxy (Z-Spar A-788 Splash Zone Epoxy, Carboline Co, St. Louis, MO USA). The epoxy was applied to the mussel shell base, avoiding the barnacle shell. To measure initial barnacle size, each tile was photographed with a Pentax K-50 digital SLR camera, with a ruler in view. The opercular length of each barnacle was measured to the nearest 0.01 mm in ImageJ (Schneider et al., 2012).

Thirty barnacles (13 small, 11 medium, and 5 large) were sacrificed to determine an initial opercular length to tissue mass relationship. These barnacles were dried for 48 h at 60 °C, and then ashed for 4 h at 500 °C. Ash-free dry mass (AFDM) was calculated as the difference between the two. The resulting equation was: $\text{mass}_{\text{mg}} = 0.610 \cdot \text{length}_{\text{mm}}^{1.92}$. There was no significant effect of size class on this relationship.

The experiment consisted of three feeding treatments (described below) and four shore height treatments (1.43, 1.30, 1.18, and 0.98 m above mean lower low water (MLLW)). The upper vertical limit of *B. glandula* on the pier pilings corresponded roughly to the 1.30 m shore height. The experiment was conducted on eight replicate 3.6 m racks, constructed of 27 mm outer diameter schedule 40 PVC pipe (Fig. 1). Each rack contained all 12 treatment combinations. The racks were hung vertically over the side of the pier and spaced haphazardly along approximately 50 m of the pier. They were attached to the pier by a pair of ropes, which ran from the top of the pier through the outermost pipe on each end of the rack. The other end of each rope was tied to a cement block that rested on the bottom of the harbor. Each rack contained three replicate 53.3 × 15.2 × 0.48 cm perforated gray PVC sheets (McMaster-Carr, Santa Fe Springs, CA), one for each feeding treatment (Fig. 1). To generate the height treatments, four tiles were attached to each sheet. Each tile contained 5 barnacles, as described above, for a total of 40 barnacles for each treatment combination. Emersion durations among the four shore heights ranged from 55% to 82% of the total experiment time (Table 1). The experiment ran from February 15 through March 26.

2.3. Feeding and monitoring

The three sheets on each rack were randomly assigned to each of three treatments: control (C), manipulated control (MC), and fed (F). Feeding manipulations occurred on 19 of the 39 days, when all barnacles were submerged (tide height > 1.43 m + MLLW) during

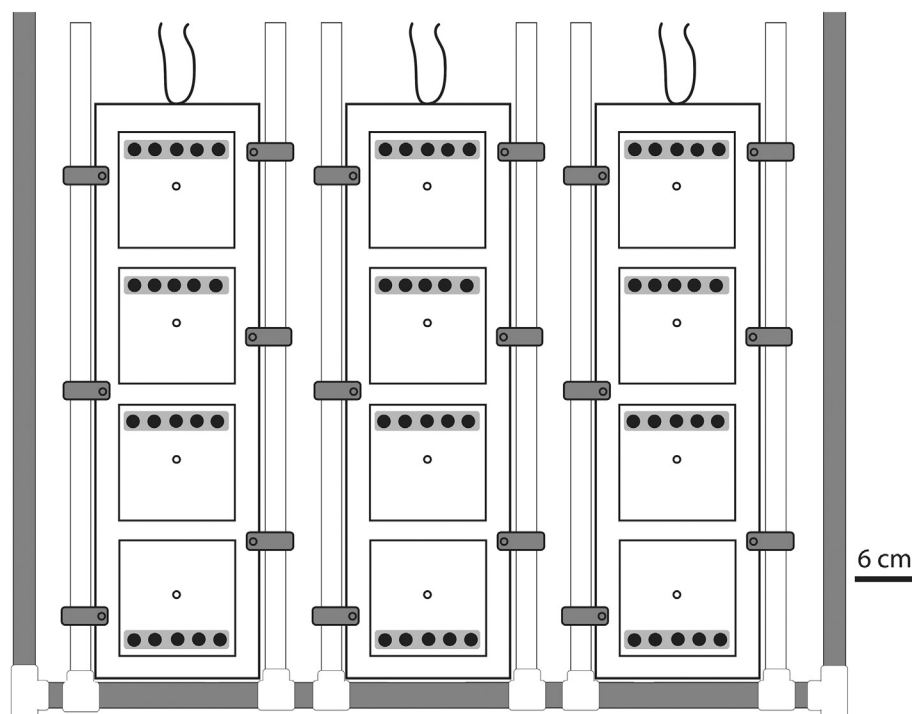


Fig. 1. Diagram of an experimental rack, constructed of PVC pipe. The rack was secured to the pier by a rope. Each rack contained three sheets of tiles. Sheets were constructed of 0.48 cm thick gray PVC, perforated with 4.8 mm holes at 8 mm intervals. Plastic rings were attached to the sides of each sheet, allowing it to slide up and down the rack for feeding and censusing barnacles. Each tile was attached to the sheet with a single machine screw (white circles). Black circles indicate locations of barnacles on each tile.

Table 1
Summary of conditions at each shore height.

Height (m)	Total hours emerged (% of experiment)	Mean (se) daily maximum temperature (°C)	% of time at or above 30 °C	% of time at or above 40 °C
1.43	765.9 (82.6%)	32.76 ^a (1.18)	7.44	1.46
1.30	693.5 (74.8%)	32.43 ^a (1.18)	6.99	1.07
1.18	626.3 (67.5%)	32.14 ^a (1.18)	5.80	0.83
0.98	511.4 (55.2%)	30.49 ^b (1.17)	3.34	0.00
Pier [†]	693.5 (74.8%)	32.04 ^a (1.17)	5.14	0.45

^{a,b}Letter indicates groups of means that are not significantly different from each other, after Tukey correction for multiple comparisons.

[†] Natural upper limit of barnacles on the pier pilings (approximately 1.30 m + MLLW).

daylight hours. Feeding durations ranged from 0.75 to 4.25 h, depending on the day and tide. During feeding, the C treatment sheets remained on the racks while the F and MC sheets were removed. These were placed into one of 4 separate 49-liter insulated coolers, filled with seawater and aerated continuously. To fit into the coolers, the sheets were rotated 90° and slid into slots at each end of the cooler. Coolers containing the F sheets were supplemented liberally with *Artemia* spp. nauplii, hatched 48–72 h prior to feeding. In the laboratory *B. glandula* grow and become reproductive on this food source (Gilman et al., 2013; Hines, 1978). All sheets were replaced on the racks before the tide level fell below + 1.43 m. Water temperatures were monitored in the coolers and ice packs added as necessary to keep temperatures from rising > 1 °C above the ocean temperature.

Mortality and shell growth were assessed during low tide on days 2, 11, 25, 33, and 39 of the experiment. On these days, each tile was photographed and we probed each barnacle's opercular plates with a dissecting needle to test for mortality. Forty-five barnacles were dead on day 2. The pattern of death was not associated with height ($X^2 = 3.6$, $df = 3$, $p = 0.31$) or feeding treatment ($X^2 = 1.6$, $df = 2$, $p = 0.43$) and thus these barnacles were assumed to have succumbed to the stress of the transplant process (e.g. Z-spar exposure, transport to field site, etc.) and were replaced with live barnacles.

To quantify food supply in the control and feeding treatments, total particulate organic matter (POM) was measured in water samples that

were collected weekly from the feeding coolers (300 mL) and directly from the harbor (1000 mL). The water samples were filtered onto a preashed glass fiber filter (Whatman GF/F, GE Healthcare, Pittsburgh, PA) and the AFDM of the filter was measured as described above. POM was chosen as *B. glandula* is an omnivorous planktivore, consuming a broad range of detritus, phytoplankton, and zooplankton (Geierman and Emlet, 2009; Riisgard and Larsen, 2010; Tallis, 2009) and thus POM should be a better estimate of food availability than chlorophyll concentration (Sanford and Menge, 2001).

To estimate the temperatures that barnacles experienced at each height, a ninth rack was established with one iButton temperature data logger (DS-1921G, Maxim Integrated, San Jose CA) placed on tiles at each of the four barnacle heights. A fifth logger was attached to the pier piling at the upper limit of barnacles growing on the pier. The loggers were wrapped in Parafilm and embedded in epoxy to enhance water-resistance and reduce reflectivity (Jones et al., 2012).

2.4. Final measurements

The experiment ended on March 26, 2015 and all barnacles were transported to the W. M. Keck Science Department. Final photographs were taken for opercular length measurements and individuals were checked for mortality. Each barnacle was carefully removed from the epoxy and its AFDM was measured, as described above. Twenty-three of the 370 surviving individuals were excluded from tissue mass analyses because either: they shattered during removal from the tiles and some tissue was lost, or not all epoxy could be removed from the outside of the shell. These 23 barnacles were not associated with any particular height or feeding treatment, based on X^2 tests ($p > 0.4$ in both tests).

2.5. Statistical methods

Temperature data was available for all four shore heights and the pier piling for Feb 16–Mar 19. The daily maximum temperature recorded from each logger was compared in SAS Proc Mixed (SAS v9.4, SAS Institute, Cary, NC) with height (fixed) and day (random) as categorical variables and the previous day's maximum temperature as a covariate to remove the autocorrelation of errors. The denominator

degrees of freedom were calculated by the Kenward-Roger method (Littell et al., 2006). To determine the frequency of thermal stress, the percent of time that each height spent at or over 30 °C and 40 °C was also calculated.

The mass of particulate organic matter (POM) was compared between the feeding treatment and the seawater control using a mixed model ANOVA in JMP v. 12 (SAS Institute, Cary NC). Sampling date and the interaction of sampling date × treatment were included as random, categorical effects.

A logistic regression in SAS Proc GLIMMIX was used to test for an association between a barnacle's probability of survival and its treatment and height. The replicate racks and a rack by treatment interaction term were included as random effects. Where main effects were significant, multiple comparisons were made using the Tukey correction.

Linear growth over the course of the experiment was negligible (mean change in operculum length = 0.053 mm), so growth was compared as the difference in final tissue mass among treatments, controlling for final operculum length. A total of 347 barnacles were included in the growth model, 20–37 for each combination of height and feeding treatment. A multifactor ANCOVA was used to test for an effect of treatment (categorical), height (continuous), or their interaction on final body mass in SAS Proc Mixed, with final operculum length as a covariate and replicate rack as a random factor. Because *B. glandula*'s body mass scales exponentially with operculum length (Gilman et al., 2013), both variables were ln-transformed prior to analysis. This transformation also resolved a significant non-normality of errors detected in a non-transformed model. However, the ln transformation of body mass changes the model equation to the form of:

$$\text{Mass} = e^{\beta_0} \cdot e^{\beta_1 \text{Height}} \cdot e^{\beta_2 \text{Food}} \cdot e^{\beta_3 \text{Height} \times \text{Food}} \cdot \text{Length}^{\beta_4}$$

No significant interactions were found between the covariate and the main effects, and so none were included in the final model. A random replicate by feeding treatment interaction term was included. The final model met assumptions of normality of errors and homogeneity of variances across the cells, after deleting one outlier with very low final tissue mass. Multiple comparisons were adjusted with the Tukey method (Westfall et al., 2011).

3. Results

Average daily maximum temperatures increased by 2.27 °C from the lowest to highest shore height (Table 1). The temperature sensor at the lowest height recorded significantly colder daily maximum temperatures than all other heights, including the sensor placed at the upper vertical limit on the pier pilings ($F_{4,99} = 4.95$, $p = 0.0011$; Tukey $p < 0.05$). However, 67.8% of the time, the loggers at the lowest and highest heights were within 0.5 °C of each other, the limit of resolution for the dataloggers we used. This means that temperatures differed by > 0.5 °C for only about 7.7 h per day. Barnacles at the highest tile height (1.43 m + MLLW) were 1.3 and 2.2 times more likely to experience temperatures over 30 °C as barnacles at the two lowest heights (1.18 m and 0.98 m respectively). Even so, the highest barnacles only spent 7.44% of their time at or above 30 °C and 1.46% of their time above 40 °C (Table 1).

Barnacles experienced feeding supplementation for a total of 18.85 h over the experiment, representing 4.33% to 11.18% of submergence time, depending on shore height. POM during supplementations averaged 0.051 g/L (0.041–0.061 95% CI), versus 0.005 g/L (−0.003–0.012 95% CI) in natural seawater, a significant increase ($F_{1,13.83} = 61.74$, $p < 0.0001$). Assuming that our control measurements were representative of natural food concentrations throughout the experiment, the supplemental feedings increased total food availability by 22.2–33.2%, depending on shore height.

Barnacle survival ranged from 67.7% to 97.5%, depending on

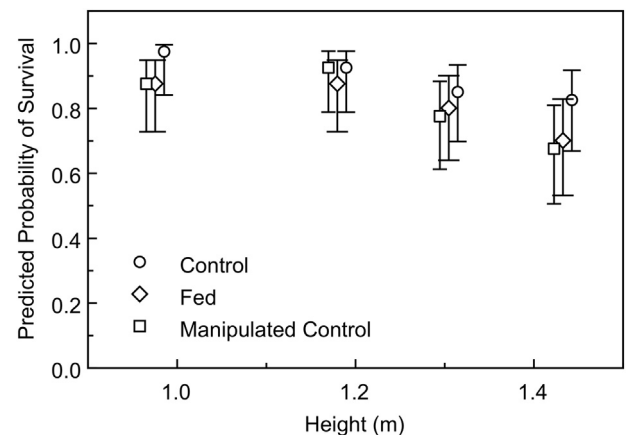


Fig. 2. Predicted probabilities (least squared means) of survival (\pm 95% CI) from the logistic regression model. Treatments are staggered slightly on the x-axis for better visibility of points ($n = 40$ barnacles per point).

Table 2
Summary of survival and final body mass models.

Fixed effects	Survival			Growth		
	F	df	P	F	df	p
Feeding treatment	2.08	2, 30.81	0.1424	8.18	2, 13.9	0.0045
Height	5.76	3, 468	0.0007	8.56	1, 322	0.0037
Treatment × height	0.35	6, 468	0.9095	0.93	2, 323	0.3956
Ln (operculum length)	n/a			221.41	1, 330	< 0.0001
Random effects	X ²	df	P	Z	df	p
Replicate	0.00	1	1.00	−0.13	1	0.8930
Replicate × treatment	0.65	1	0.4193	0.75	1	0.4535

height and feeding treatment (Fig. 2). Survival decreased with increasing shore height (Table 2), although only the highest height was significantly different from the lowest two heights ($p < 0.05$, Tukey correction). There was a tendency for greater survival in the control than the manipulated treatments (Fig. 2), but this difference was not significant. Barnacle mortality was greatest between the third and fourth census dates (3/12–3/20). Between these dates, temperatures at the three highest heights exceeded 40 °C for four days in a row.

The ANCOVA model of body mass revealed significant effects of both height and feeding treatment on barnacle final tissue mass (Table 2). When compared at an average height and operculum length, the fed treatment was 28.6% and 20.7% heavier than the control ($p = 0.0102$) and manipulated control ($p = 0.003$), respectively. The two control treatments did not differ significantly from each other ($p > 0.05$). The slope of height in the ANCOVA was negative ($e^{-0.327 \text{ht}}$, roughly equivalent to a linear slope of $-4.3 \text{ mg} \cdot \text{m}^{-1}$), indicating barnacles had smaller final masses higher on the shore. Comparison of the back-transformed LS Means calculated at each combination of feeding treatment and shore height showed a pattern of greater effects of feeding on final mass at lower shore heights than higher shore heights (Fig. 3), although the interaction between height and feeding treatment was not significant (Table 2). The fed treatment was 31.5–37.4% heavier than either control at the lowest height, but only 8.8–19.3% heavier than controls at the highest height.

Based on our initial sample of barnacles at the start of the experiment, the 4.14 mm barnacle depicted in Fig. 3 would have had an initial dry tissue mass of 9.1 mg, suggesting that barnacles increased in mass at all heights, except perhaps for the manipulated control at the highest height (Fig. 3). When compared to this initial body mass, fed barnacles increased their dry tissue mass by 62% at the lowest shore height, but

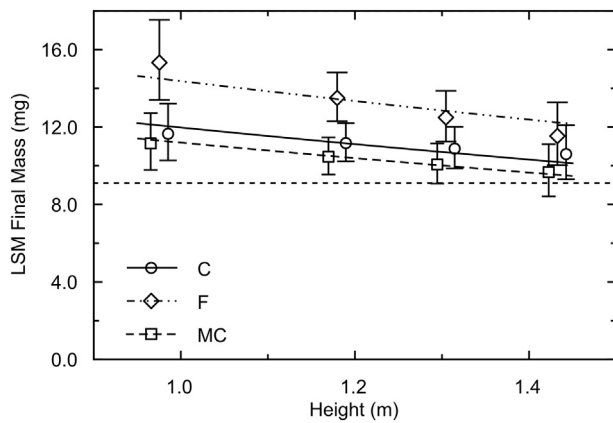


Fig. 3. Back-transformed least squared mean (LSM) final mass (\pm 95% CI) for each combination of feeding and height, from the full ANCOVA model ($n = 20$ –37 barnacles per mean). Treatments are staggered slightly on the x-axis for better visibility of points. LSM mass values are calculated for a barnacle of 4.14 mm opercular diameter, representing the average opercular length at the end of the experiment. The dashed horizontal line indicates the estimated initial mass of a barnacle of this opercular size, from the group of barnacles sacrificed at the start of the experiment. The three other lines reflect the model predictions for each feeding treatment, without the (non-significant) treatment \times height interaction term.

only 19.4% at the highest shore height.

4. Discussion

The abiotic stresses of low tide are commonly thought to reduce the success of organisms at higher shore levels (Connor and Robles, 2015; Levinton, 2014; Petes et al., 2008; Somero, 2002), yet it has not been established whether these stresses limit survival directly or interact with energy limitation (Somero, 2002). This study manipulated the food supply of intertidal barnacles living near their upper vertical limit. Our results indicate that supplemental food increased final tissue mass significantly at all shore heights, suggesting that barnacles at and above their upper vertical limits benefit from an increased food supply, in spite of greater abiotic stress.

Although we had hypothesized a greater benefit of supplemental food for high shore individuals, our results suggest that increased food supplies benefited barnacles equally at all shore heights. Our original hypothesis was based on an assumption that longer emersion times on the high shore would lead to greater food limitation and thus a greater benefit from exposure to short periods of high food concentration. Instead our results suggest that all barnacles in the experiment faced energy limitation. This energy limitation likely reflects a combination of restricted feeding time and low overall food supply. Higher shore heights are frequently associated with lower growth due to reduced feeding times (Gillmor, 1982), and even our lowest shore height was submerged for < 45% of the experiment. But the high food concentration in our supplemental feedings also increased the total food supply by 22–33%, even though these feedings were only 4–11% of submergence time. Thus the supplemental feedings represented a meaningful increase in food supply at all shore heights examined. *Balanus glandula*'s vertical distribution extends much lower on the shore than the heights used in this experiment (Glynn, 1965), and it may be that there are lower shore heights, with greater immersion times, that would show less benefit from supplemental food.

Our results also suggest a trend of reduced benefits of supplemental feeding on the high shore. Supplemental feeding increased body mass by up to 37% at the lowest shore height, but < 20% at the highest, although this pattern was not statistically significant. This trend could reflect a stress-induced reduction in feeding activity. Repeated daily exposure to high temperatures at low tide is known to inhibit feeding during immersion in several intertidal species (Miller et al., 2014;

Pincebourde et al., 2008; Yamane and Gilman, 2009) and has been observed in the laboratory for *B. glandula* as well (D. Bimstein and S. Gilman, unpubl. data). The role of emersion stress in inhibiting subsequent feeding activity has generally been underappreciated in thermal ecology.

Survival was significantly lower at our highest shore height than the lowest; yet, food supply did not affect survival. Moreover, survival exceeded 68% at all shore heights, even though the highest of our four shore heights was above the upper limit of *B. glandula*. These results can be explained in part by the fact that adults were used instead of juveniles or new recruits. Because *B. glandula* is a sessile species, adults can only be found in locations where earlier life stages can survive, even if adults themselves could tolerate higher shore heights. Thus the tolerances of early life stages are likely more relevant to determining upper vertical limits of intertidal species than adult tolerance, and in many species, early life stages are less tolerant of stress than adults (Sokolova et al., 2012). Indeed, Foster (1971a) reported that larvae of the high intertidal Atlantic barnacle *Semibalanus balanoides* routinely settled > 20 cm above adults, but then died off within their first year. Survival of newly settled *B. glandula* can be quite low, with mortality often attributed to temperature and/or desiccation stress (Gosselin and Jones, 2010), but also influenced by individual energy reserves (Emlet and Sadro, 2006; Gosselin and Qian, 1996). This experiment was originally planned for newly settled individuals, but was changed to adults due to very low levels of barnacle recruitment at our field sites in southern California in the past few years. Future work on this species should compare the tolerances of both adults and juveniles to emersion stress.

Finally, average daily maximum temperature was a poor indicator of emersion stress in this study. The three highest shore heights did not differ significantly in average daily maximum temperature, yet there were significant differences in both survival and final mass among these three heights. Convergence in daily maximum temperature among the highest shore heights is not surprising, given that daily low tide exposures were as long as 7.6 h at even the lowest of the four heights and Helmuth (1998) found that intertidal animals can reach a steady-state with the terrestrial climate within as little as 30 min of emersion. Indeed, the highest and lowest heights spent nearly 70% of each day at near-identical temperatures. Clearly, the reductions in survival and growth observed at higher shore heights were driven by something other than the absolute maximum body temperature reached each day. Temperature, particularly daily maximum temperature, is frequently used as a proxy for emersion stress in both intertidal ecology and physiology (e.g., Fitzgerald-Dehoog et al., 2012; Harley and Helmuth, 2003; Helmuth et al., 2006b; Kroeker et al., 2016; Stillman and Somero, 2000). Our results suggest that average daily maximum temperature does not reflect the magnitude of emersion stress experienced by barnacles.

The lower survival and growth could have been driven either by aspects of thermal stress unrelated to average daily maximum temperature or by non-thermal sources of emersion stress. In the first case, barnacles may be more sensitive to extreme thermal events, rather than to routine daily maxima (Gaines and Denny, 1993; Gilman et al., 2015). While the highest shore height experienced an average daily maximum temperature only 0.62 °C greater than the third highest height, those barnacles were 1.28 times more likely to experience temperatures above 30 °C and 1.76 times more likely to experience temperatures over 40 °C. Those extreme events could be more important for survival, and possibly growth, than the average daily maximum experienced. Another possibility is that the differences we observed were driven by differences in the overall duration of emersion at different heights. The highest shore height averaged 1.9 more hours of low tide exposure each day than the third highest height. The longer emersion times, even in the absence of clear thermal differences, may have reduced barnacle growth (Gillmor, 1982). Finally, other abiotic stressors, such as hypoxia, ultraviolet radiation, or desiccation may have contributed to the observed performance differences. Desiccation is the most likely of

these as it has been shown to reduce the survival of other high shore barnacle species in laboratory experiments (Foster, 1971b). Hypoxia is unlikely to play a role as *B. glandula* can consume oxygen at greater rates during emersion than when immersed (S. Gilman, unpubl. data). There is also little evidence for an effect of UV radiation on *B. glandula* (Gosselin and Jones, 2010).

In conclusion, this study sought to test the hypothesis that reduced food availability limits the survival and growth of high shore intertidal animals. There were no effects of food supplementation on survival, but clear increases in body mass with supplementation at all shore heights. Our results suggest that energy limitation acts in conjunction with emersion stress to constrain the growth of high shore individuals of the barnacle *B. glandula*. Furthermore, our results suggest that energy limitation, driven by food limitation and/or feeding inhibition, may influence the location of upper vertical limits in many species. Thus accurate predictions of species' responses to climate change will require a consideration of the direct effects of climate in the context of climate-related changes in resources (Gilman et al., 2010). This study also demonstrates that it is possible to directly manipulate the food supply of intertidal planktivores in the field. More studies like this one are necessary to fully characterize the mechanisms by which emersion stress limits success on rocky intertidal shores.

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